# Anatomy and phylogeny of the gavialoid crocodylian *Eosuchus lerichei* from the Paleocene of Europe

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Originally designated by Dollo in 1907, the holotype of *Eosuchus lerichei* has never been carefully described but simply cited and compared in a number of papers. This work is an attempt to fill this gap and to place this taxon in a cladistic phylogenetic context. *E. lerichei* can be considered a valid basal gavialoid from late Paleocene of North Western Europe, sharing the presence of extremely enlarged foramina aerea on quadrates with the coeval *Eosuchus minor* from eastern North America (formerly described as *Gavialis minor*). These two species can be considered sister taxa and, for priority reason, they should be both ascribed to genus *Eosuchus*. The results of the cladistic analysis show that the European species possess characters that can be considered as slightly derived if compared to those of its American relative, suggesting an eastward dispersion from North America before the Paleocene–Eocene boundary and before the full opening of the Atlantic Ocean or local evolution from a basal gavialoid stock similar to *E. minor*. Both species of *Eosuchus* come from marine outcrops and represent a further evidence for the salt-water tolerance of the earliest stages of Gavialoidea evolutionary history. Despite the present endemicity of the only living gharial, *Gavialis gangeticus*, the historical biogeography of gavialoids shows a lost global distribution and reveals several transoceanic dispersals.

Key words: Crocodylia, Gavialidae, *Eosuchus*, transoceanic dispersal, osmoregulation, Paleocene, Jeumont, Erquelinnes.

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## Introduction

The taxon *Eosuchus lerichei* Dollo, 1907 was introduced in a brief and schematic description of a new crocodylian skull discovered at the French-Belgian border (Dollo 1907). The planned "figured description with references and general conclusions" was never published by its author and for decades the best source of information about this taxon has been the comparative description of *Dollosuchus dixoni* (Owen, 1850) provided by Swinton (1937), who also published for the first time some pictures of *E. lerichei*.

As noted by Broom (1925), for priority reasons the name *Eosuchus* is not available for the Triassic diapsid from Southern Africa described, as a new genus and new species, by Watson in 1912, a few years after the Dollo paper about the European crocodylian (1907); the proper name of the African diapsid is therefore *Noteosuchus colletti* (Watson, 1912) and not *Eosuchus colletti*.

During the past century, *Eosuchus lerichei* has been considered as belonging to Tomistomidae (Kuhn 1936; who regarded this taxon as synonym of Thoracosauridae), Thoracosaurinae (Steel 1973; who considered this taxon as synonym of Tomistomidae and Tomistominae), Crocodylidae (Swinton 1937), or Gavialidae (Vasse 1993), while the generic name of *Eosuchus* has been used by Kuhn (1936) and Swinton (1937) for *Gavialis dixoni* Owen, 1850, the crocodylian from Maransart carefully described later on by Swinton (1937) and placed in the new genus *Dollosuchus*.

Brochu (1997) wrote that *Eosuchus lerichei* is so similar to *Crocodylus spenceri* Buckland, 1836 [= *Kentisuchus spenceri*] that could represent this taxon but more recently the same author (2001a, b) suggested that it represents a gavialoid and placed it (misspelt as "*E. lerelichii*") among the Gavialoidea in a figure concerning the phylogenetic relationships of this group (Brochu 2003). Such a phylogenetic relationship has been recently confirmed by the cladistic analysis in a paper (Brochu in press) that comparatively describes *E. lerichei* in order to re-evaluate the taxonomic allocation of *Thecachampsoides minor* (Marsh, 1870) from the Paleocene–early Eocene of New Jersey. According to that paper, *T. minor* (formerly described by Marsh as *Gavialis minor*) and *E. lerichei* share at least three morphological characters allowing to group them in the genus *Eosuchus*; this genus represents a basal Gavialoidea more derived than *Eothoracosaurus* and *Thoracosaurus*.

The aim of the present paper is to redescribe the anatomy of *Eosuchus lerichei*, whose potential taxonomic and phylogenetic relevance (due to its age and preservation), as well as

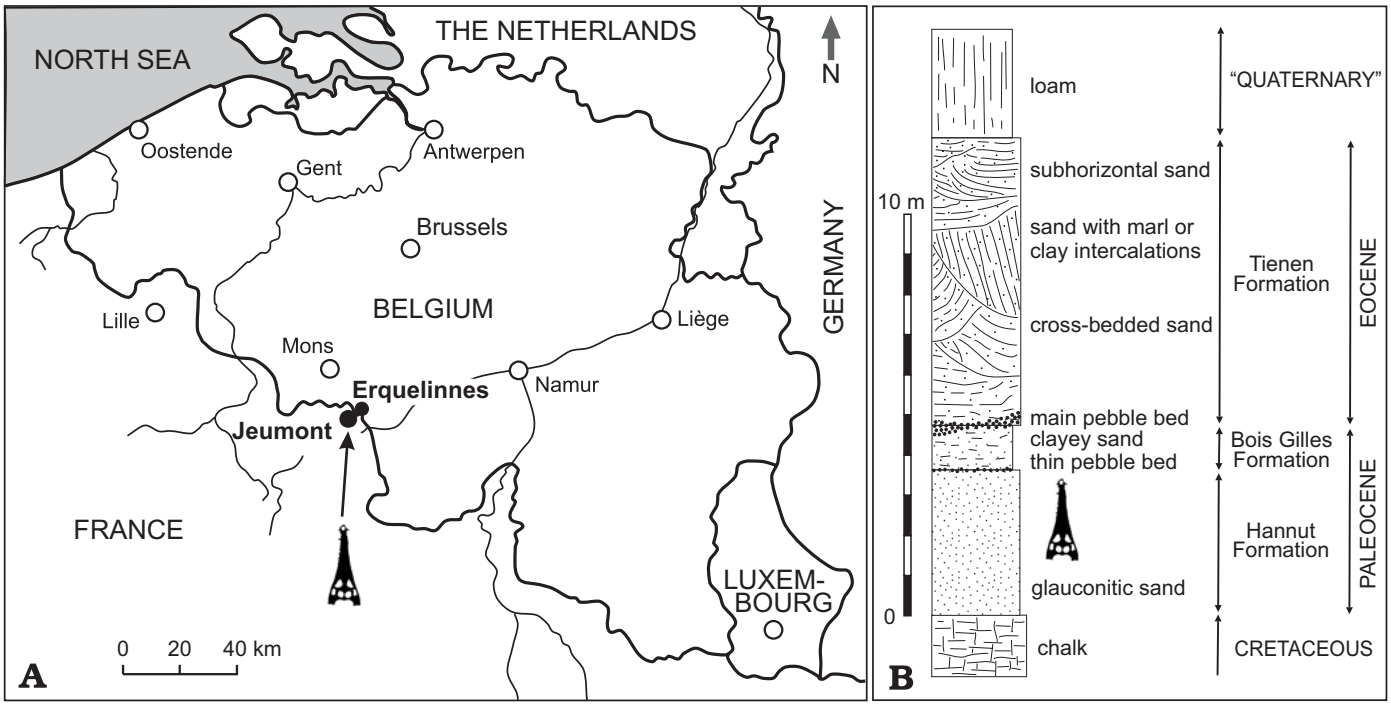


Fig. 1. **A**. Geographic location of the Paleocene–Eocene vertebrate localities of Jeumont and Erquelinnes at the French-Belgian border. **B**. Schematic representation of the section made by de Heinzelin in 1946 and 1954. The remains of *Eosuchus lerichei* come from the glauconitic sand belonging to the late Paleocene Hannut Formation.

its biogeographic implications, sharply contrast with the fragmentary character of the available published information. Its stratigraphic position and age are also reconsidered on the basis of new relevant micropaleontological information (De Coninck et al. 1981; Steurbaut 1998).

*Institutional abbreviations*.—ANSP, Academy of Natural Sciences (Philadelphia); IRSNB, Institut royal des Sciences naturelles de Belgique (Bruxelles); SMNK, Staatliches Museum für Naturkunde (Karlsruhe); USNM, United States National Museum of Natural History (Washington, DC); YPM, Yale Peabody Museum (New Heaven).

# Geological setting

The remains of *Eosuchus lerichei* were discovered in 1907 in the sand quarries of Mr. Martial Dusart and son, located at Jeumont, 10 km east of Maubeuge (Département du Nord, France, Fig. 1A) and few meters far from the French-Belgian border. These fossiliferous strata form part of the well-known outcrop area of Erquelinnes, extending a few km northward on the Belgian territory (Dollo 1907; Teilhard de Chardin 1927; Sigogneau-Russell and de Heinzelin 1979). According to Dollo (1907), the crocodile remains were found in the lower Landenian deposits, which at that time were included in the Eocene. The stratigraphic information on the Erquelinnes area was pieced together by de Heinzelin (in Sigogneau-Russell and de Heinzelin 1979), who was able to decipher the stratigraphic context of the different vertebrate finds.

According to de Heinzelin, in the Jeumont-Erquelinnes quarry complex, the Paleocene–Eocene transition was preserved under 3 m of "Quaternary" loam (Fig. 1B). The lowermost Eocene is represented by fluviatile deposits of the Tienen Formation containing remains of terrestrial mammals, fresh-water chelonians and crocodylians. The underlying strata are represented by the Bois-Gilles Sand Formation, a shallow marine sand unit of terminal Paleocene age, rich in shark teeth and belonging to the calcareous nannoplankton zone NP9 (de Coninck et al. 1981).

The skull of *Eosuchus lerichei*, as well as several skeletons of *Champsosaurus* and shells of the turtle *Erquelinnesia* were collected in a shallow marine non-calcareous glauconitic sand unit underlying the Bois-Gilles Formation (unit B of Sigogneau-Russell and de Heinzelin 1979). This unit, overlying the Upper Cretaceous chalk, was subsequently identified as the Grandglise Sand Member, belonging to the Hannut Formation (Steurbaut 1998). Micropaleontological investigations carried out by de Coninck et al. (1981) showed that the *Eosuchus*-bearing beds belong to the lower part of the *Apectodinium hyperacanthum* dinoflagellate cyst zone of Powell (1992), which according to Steurbaut (1998) corresponds to zone NP8 and points to a mid-Thanetian age (*sensu* Berggren et al. 1995). However, despite these very precise age assessments, some authors (Vasse 1993; Jouve 2004) still assign an Eocene age to the *E. lerichei* remains.

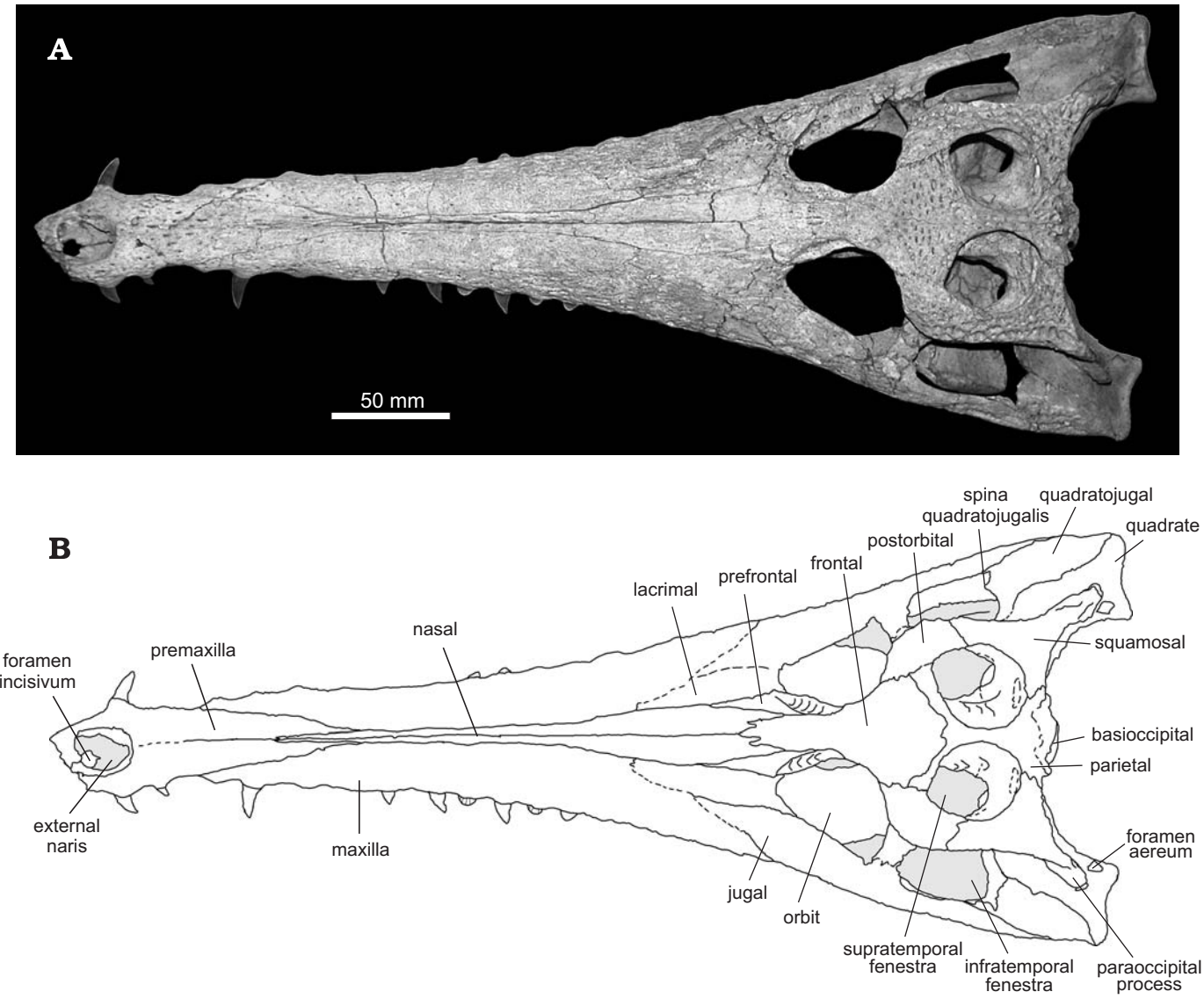


Fig. 2. Holotype of *Eosuchus lerichei* Dollo, 1907. IRSNB R 48, Jeumont, France, late Paleocene, skull in dorsal view (**A**) and explanatory drawing of the same (**B**).

# Systematic paleontology

Eusuchia Huxley, 1875

Crocodylia Gmelin, 1789

Gavialoidea Hay, 1930

Genus *Eosuchus* Dollo, 1907

*Type species*: *Eosuchus lerichei* Dollo, 1907.

*Species assigned*.—*Eosuchus lerichei* Dollo, 1907 and *Eosuchus minor* (Marsh, 1870).

*Definition*.—A stem-based group name including the type species, *E. lerichei* Dollo, 1907, plus *E. minor* (Marsh, 1870) and all gavialoids more closely related to them than to *Eogavialis africanus*.

*Emended diagnosis*.—A basal gavialoid that can be differentiated from any other crocodylian by the following combination of characters: an unusually enlarged foramen aereum, dentary alveoli arranged in couplets, evident "quadrate crest" ventrally developed at least on quadrates and pterygoids, nasals reaching and deeply entering between premaxillae, W-shaped basioccipital tuberosity. A further peculiarity could be represented by the presence of an unusual "step-like" widening of the orbital margin of prefrontal.

## *Eosuchus lerichei* Dollo, 1907

*Holotype*: Specimen IRSNB R 49 is represented by a nearly complete skull (Figs. 2–4), an incomplete lower jaws (Fig. 5), the axis (Fig. 6A), three cervical vertebrae, an isolated neural arch, three ribs, a fragmentary ulna and radius, a carpal element and fourteen osteoderms (or their fragments; Fig. 6B). All the remains seem to belong to one single individual.

*Type locality*: Jeumont (Maubeuge, Nord Department), France. The locality, few meters far from the Franco-Belgian border, is part of the well known fossiliferous area of Erquelinnes, Belgium.

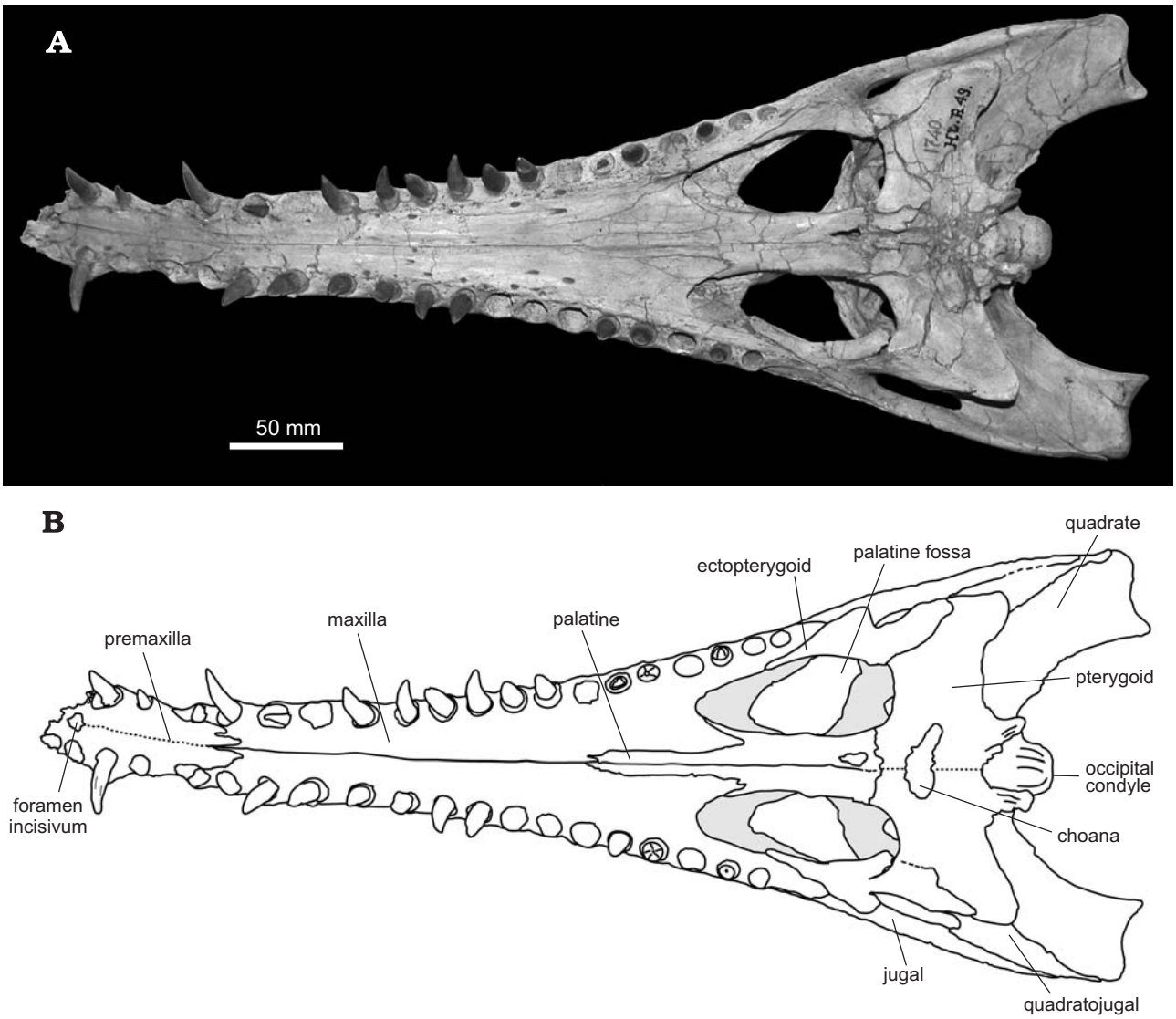


Fig. 3. Holotype of *Eosuchus lerichei* Dollo, 1907. IRSNB R 48, Jeumont, France, late Paleocene, skull in ventral view (**A**) and explanatory drawing of the same (**B**).

*Horizon and age*: Grandglise Member, Hannut Formation, Thanetian, upper Paleocene.

*Emended diagnosis*.—*Eosuchus lerichei* can be distinguished from *E. minor* by the axis neural arch devoid of any lateral process, a relatively slender postorbital bar, the presence of the triple junction between frontal, parietal and postorbital on the skull table, ectopterygoids separated from the toothrow by maxilla and palatine anterior process showing a irregular morphology that can be assimilated to a U-shaped condition. Nasals are relatively narrower and frontal process slightly longer than in *E. minor*.

Moreover, the holotype—and only known specimen—shows 5 premaxillary (see description), 16/17 maxillary and at least 22 dentary teeth; the symphysis reaches posteriorly the sixteenth tooth position; teeth have a peculiar shape since they do not show any evident labio-lingual compression or mesio-distal keels but several ridges of similar development occurring on the entire crown surface.

## *Description*

### Skull

*Preservation, form, and general features*.—The skull is relatively complete, lacking only part of the anteriormost portion of the premaxillae. The general morphology is perfectly readable and allows a detailed description, even though other elements are slightly incomplete (i.e., quadratojugals, basisphenoid rostrum) or crushed (pterygoids), and the skull shows an evident dorso-ventral compression: the rostrum is slightly bent upward and leftward, pterygoids are dorsally displaced, the postorbital bars are nearly L-shaped (due to the lowering of the skull table) and the skull is slightly asymmetrical in occipital view. A minor asymmetry shown by the skull when observed in dorsal view (for example, the left quadrate does not reach the posterior extent of the right one) could be indirectly related to such compression.

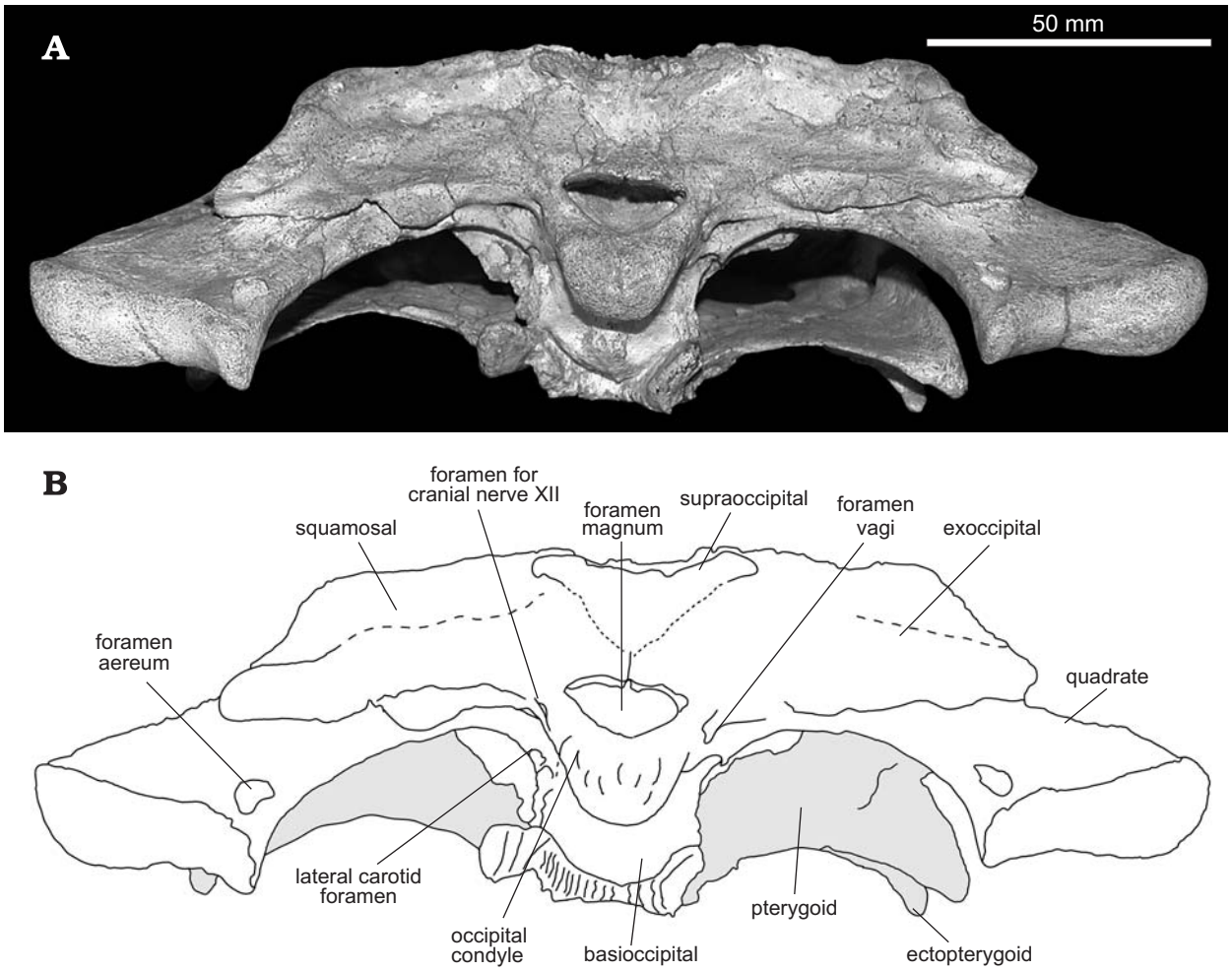


Fig. 4. Holotype of *Eosuchus lerichei* Dollo, 1907. IRSNB R 48, Jeumont, France, late Paleocene, skull in occipital view (**A**) and explanatory drawing of the same (**B**).

The skull is distinctly slender snouted and elongated although not as elongated as in truly "longirostrine" taxa as *Thoracosaurus* or *Gavialis*, its total length (from the tip of the premaxillae to the level of quadrates) is 47.1 cm, its maximum width (between the quadrates) is 18.6 cm.

The lateral margin of the rostrum is modestly festooned in dorsal view (mainly in the anterior area) but not in lateral view; the widest lateral concavity corresponds to the premaxilla-maxilla suture. Nearly all the bone surface is sculptured but only the elements of the skull table and the lateral surface of quadratojugals are heavily pitted. The skull table is nearly rectangular and with rather straight sides and long squamosal prongs (character 140-status 1; the indication of character status will be abbreviated in the following format: 140-1) in dorsal view; slightly sloping in occipital view (123-0; actually, the skull table is somewhat undulating and the sloping could have been partly influenced by the dorsoventral compression that acted more heavily on the sides of the skull than on the centre).

*Cranial fenestrae and openings*.—The external naris is entirely surrounded by the premaxillae without the development of any ridge or notch at the narial rim. Narial aperture projects dorsally (79-1), it is longer than wide and approximately circular (161-0) or better, vaguely trapezoidal (with slightly convex sides and a wider basis anteriorly placed). The orbits have a semicircular shape (with the jugal margin nearly straight) and their margin is slightly upturned (103-1); a small notch is present at the postero-lateral corner (since the notch is not prominent, character 139 has been scored as 0). The supratemporal fenestrae are delimited by parietal, postorbital and squamosal, with no frontal participation, wide (87-0), slightly smaller than orbits, drop shaped (longer than wide and with main axes divergent), with relatively sharp edges and with smooth antero-medial corner (92-1). Their inner surface is fractured and the sutures are not entirely visible; it is possible to see part of the sutures between laterosphenoid and quadrate and between quadrate and squamosal; the temporal canals are obliterated by matrix; the parietal surface seems to be imperforate (104-0); the inner medial walls are not gradually sloping but nearly form a plateau-like surface. The infratemporal fenestrae are limited by postorbitals, jugals and quadratojugals; their size is smaller than that of the orbits, while the shape—roughly trapezoidal

—is slightly altered by the dorso-ventral deformation of the skull and by the incompleteness of the quadratojugals (the left one in particular); the posterior margin of infratemporal fenestra seems to be formed by quadratojugals (75-0). The morphology of the posterior margin of otic aperture cannot be evaluated since it is damaged on the left side of the skull and deformed on the right one (where it is apparently bowed; 102-?). Lateral Eustachian canals open dorsal to medial eustachian canal (147-0). On the occipital surface of the skull, open posttemporal fenestrae are delimited by squamosal, parietal, exoccipital and supraoccipital; they are hardly visible because of the dorso-ventral compression and the filling matrix. The foramen magnum opens between the exoccipitals and the basioccipital (occipital condyle); its shape (elliptical, wider than tall, and with the dorsal edge less convex than the ventral one) has been probably slightly distorted because of the general deformation of the skull. The incisive foramen opens between the premaxillae and its anterior margin is lateral to second alveolus (153-0); it is rather small (124-0) and drop shaped. Suborbital fenestrae are wide and almond-shaped; the anterior edge reaches, on both sides, the posterior margin of the fourteenth tooth position; the lateral sides are straight (105-0) and there are no notches at the posterior corners (88-0). The choanae are entirely surrounded by the pterygoids (71-1) and are placed relatively close to the pterygoid-palatine suture (the anterior position of choanae had been already noticed by Dollo 1907: 85, "choanes moins reculées vers l'occiput que les Eusuchiens actuels"); even if the presence of several fractures and the deformation of the area alter the original shape, the choanae seem to project postero-ventrally (72-0), their anterior and lateral margin seems to be flush with the pterygoid surface (73-0), while the posterior margin is not deeply notched (107-0); a septum was present but, since it is broken off, it is not possible to evaluate its development (152-?).

*Premaxillae*.—The anteriormost tip of the premaxillae is lacking (the left element is particularly incomplete). Four complete alveoli are preserved on the right and two on the left, but due to the presence of a cavity in the broken anteriormost area, we can assume that 5 is the number of premaxillary teeth (97-0); both Dollo (1907: 84) and Swinton (1937: 43) reported the presence of 5 premaxillary teeth. Two teeth are preserved on the left premaxilla and one on the right. The largest alveolus is the fourth. The dorsal premaxillary processes meet at the midline, exclude the nasal from the external nares (95-2), and extend to the level of the fourth maxillary alveolus (145-1); the ventral premaxillary processes extend to the posterior margin of the second maxillary alveolus. The premaxillary-maxillary suture on the palatal surface is W-shaped and posteriorly acute. The dorsal surface of premaxillae is smooth at the postero-lateral corner of naris (142-0).

*Maxillae*.—Sixteen maxillary alveoli are preserved on the right side (9 with teeth) and 17 on the left (10 with teeth). Such a disparity, commonly seen in longirostrine taxa, could be due to the presence of an additional alveolus on the left side, or the absence of an alveolus on the right one. The widest interalveolar space is the second, and the interalveolar distance is usually shorter than the mesio-distal alveolar diameter. The dorsal surface shows neither swelling corresponding to the largest tooth nor canthi rostralii (143-0). The maxillary foramen for the maxillary ramus of the fifth cranial nerve is small (111-0). Large foramina are present on the palatal surface of maxilla. The maxillary toothrow slightly curves medially (135-0).

*Nasals*.—The anteriormost two thirds of the nasals are quite slender and they widen considerably between lacrimals. They do not reach the external naris and terminate anteriorly at the level of the second maxillary tooth position. Posteriorly, they extend beyond the anterior margin of the orbits. The suture with frontal is characterized by a deep interdigitation. There is no trace of "boss" and therefore the dorsal surface of the skull curves smoothly (101-0).

*Lacrimals*.—The lacrimals edges are medially concave along the nasals and probably laterally convex, although the suture with maxilla cannot be followed with confidence. The lacrimals are longer than the prefrontals (117-0). Due to the presence of several fractures, the maxilla-lacrimal suture is not visible with confidence; however, it seems that a relevant posterior maxillary process is not present (character 93 has been tentatively scored as 0). Neither canthi rostralii nor preorbital ridges are developed. The lacrimal duct is visible only in the right orbit; it has an elliptic section (main axis horizontal) and is located in the inner medial border of the orbit at the anterolateral left corner; its left side abuts the suture between prefrontal and lacrimal.

*Prefrontals*.—The prefrontals are elongated and narrow in dorsal view. Their orbital margin is characterized by the presence of a distinct and very peculiar "step" (see Fig. 6C) whose surface shows small ridges and depressions (the pattern is different from that of the pitted skull surface). The interorbital space is therefore slightly, but distinctly, convex in dorsal view. The prefrontals do not meet medially (100-1). The prefrontal pillars are damaged and their shape cannot be evaluated; however their dorsal half is not expanded anteroposteriorly (137-0).

*Jugals*.—The right jugal is deformed and partly displaced into the orbit. The left jugal is better preserved. Jugals dorsal margins, delimiting the lateral rims of the orbits, are each raised in a low "ridge" that terminates a little before the postorbital bar, producing a small notch at the postero-lateral corner of the orbit in dorsal view. The anterior sutures of both jugals are not easily perceptible. The medial jugal foramen anterior to postorbital bar is small (120-0). An unsculptured dorsal process of the jugals forms the ventral portion of the postorbital bars; this process excludes the postorbital from the basis of the bar; it reaches approximately one third of the postorbital bar and it has a vaguely horizontal edge.

*Frontal*.—The frontal process is relatively robust and extends anteriorly well beyond the orbits. The frontoparietal

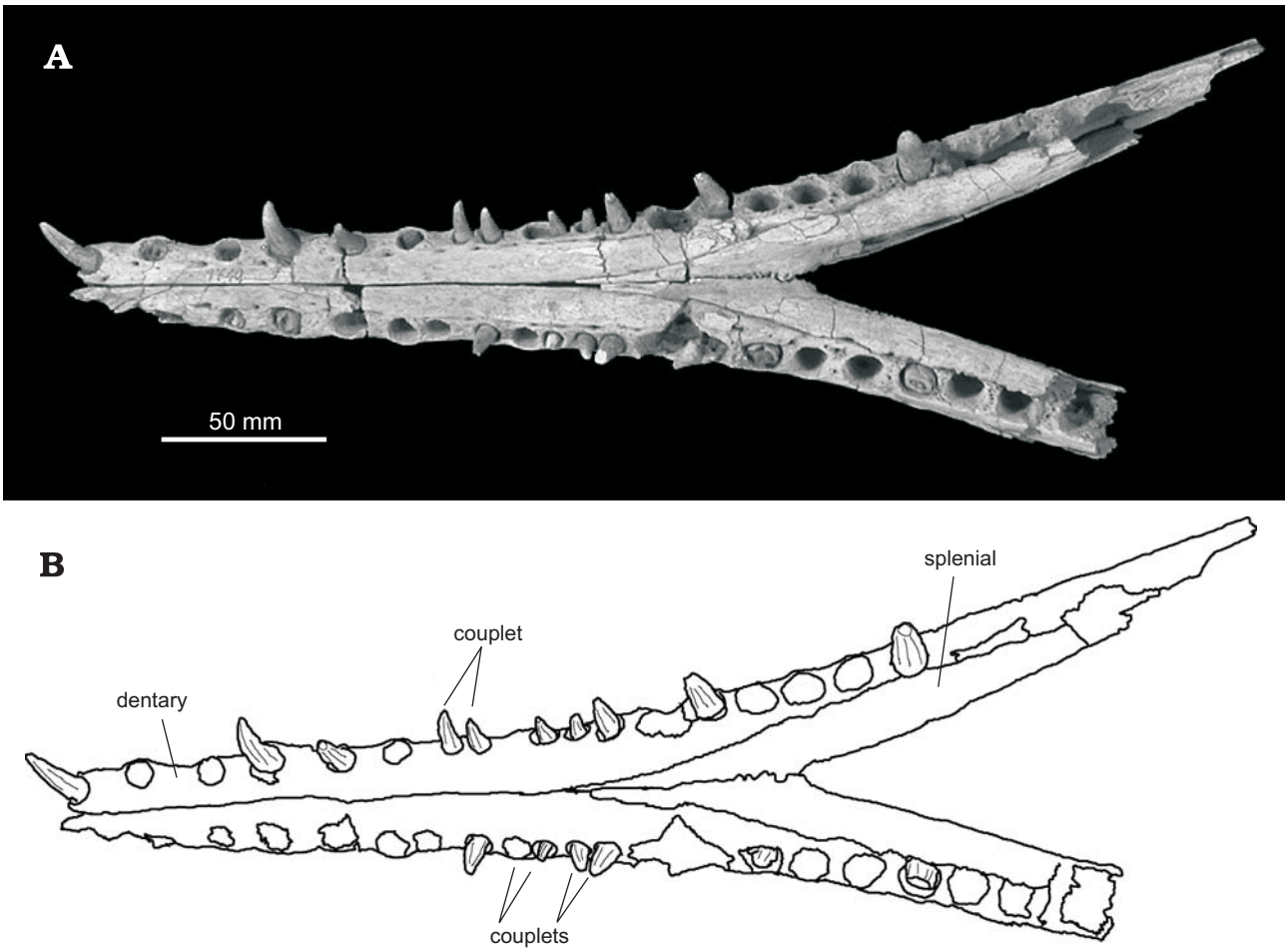


Fig. 5. Holotype of *Eosuchus lerichei* Dollo, 1907. IRSNB R 48, Jeumont, France, late Paleocene, lower jaw in dorsal view (**A**) and explanatory drawing of the same (**B**).

suture is deeply concave anteriorly (86-0) and does not intersect the supratemporal fenestrae (81-2; therefore the triple junction between frontal, parietal and postorbital is on the skull table).

*Postorbitals*.—Probably due to a strong dorso-ventral compression, the postorbitals are bent downward while the postorbital bars are strongly deformed and bent inward ("L" shaped; Fig. 6C). Postorbital bars are relatively slender (70-1; see discussion) and although apparently inset from jugal's lateral margin (because of the strong deformation of the region), they were probably flush with lateral jugal surface in an undeformed condition (146-0). The postorbital-squamosal suture is oriented ventrally on the lateral margin of skull table (163-0). The anterolateral corners of postorbitals are broadly curved.

*Squamosals*.—The squamosals do not seem to be as affected by compression as postorbitals. They do not extend ventro-laterally to lateral extent of paraoccipital process (150-0). The squamosal grooves for the external ear valve diverge gently anteriorly (84-1). The squamosal-quadrate sutures extend dorsally along the posterior margin of external auditory meatus (132-0). The squamosal prongs are rather long (longer than in Recent *Gavialis* but not as long as in South American gavialoids; Brochu and Rincón 2004). The posterior squamosal rim extends beyond the occipital surface.

*Parietal*.—The parietal constitutes the anterior, medial and part of the posterior margin of each supratemporal fenestra; the sutures with squamosals and supraoccipital, as well as the sutures with the elements involved in the walls of the supratemporal fenestrae are not perceivable with confidence.

*Quadratojugals*.—The anterior margins of the quadratojugals are damaged: only the lateral portion of the anterior margin of the left quadratojugal is preserved, and it bears a moderately developed anterior spine (69-0) located close to posterior angle of infratemporal fenestra (114-0); the quadratojugals seem to bear a relatively long process along the lower temporal bar (83-0).

*Quadrates*.—The quadrates bear large foramina aerea (maximum width of 5 mm approx.; Fig. 6D), flush with the quadrate surface, placed relatively near the medial edge and not distinctly inset from the margin of the retroarticular process (121-0). The medial hemicondyle is small and ventrally

reflected (112-0). The ventral surface of the quadrate is characterized by a prominent crest (called the "quadrate crest" by Brochu in press) extending to the pterygoids.

*Supraoccipital*.—The parietal-supraoccipital suture is partly visible in dorsal view and, even if the supraoccipital is crushed, the latter seems to be slightly exposed in dorsal view (82-0); its occipital surface is smooth.

*Basioccipital*.—The basioccipital forms the occipital condyle and the ventral border of foramen magnum; it is rather large and not tall (probably dorso-ventrally compressed and deformed). Since basioccipital sutures are not clearly visible, the relationships with the surrounding bones have not been described. An irregular crest forms a W-shaped tuberosity partly visible in occipito-ventral view because lateral branches of the W are hidden by pterygoids slightly displaced by the deformation of the region.

*Basisphenoid*.—The basisphenoid exposure ventral to the basioccipital has not been evaluated due to the absence of well-defined sutures in that area. As a consequence, the braincase morphology and the Eustachian system arrangement are difficult to assess.

*Exoccipitals*.—Exoccipitals surround the dorsal and lateral walls of the foramen magnum (whose shape is distorted by dorso-ventral compression; each is twice as wide as high); descending processes project ventrally and participate in the basioccipital tubera (151-1); the paraoccipital processes are significantly wider than the skull table, and lack a boss (141-1). The inter-exoccipital suture is not elevated into a ridge. Cranio-quadrate canals are hidden by exoccipital laminae in occipital view.

*Palatines*.—The palatines are characterized by anterior processes that extend well beyond the anterior end of suborbital fenestra (110-0). The palatine process reaches the level of the tenth maxillary alveolus and is asymmetrically developed and not invaginate (108-0; the posterior small process of the left maxillary is here interpreted as an irregularity of the suture) and they show a particularly narrowed U-shaped condition (118-0; see discussion). The lateral edges of the palatines are parallel posteriorly between the suborbital fenestrae (90-0) and do not bear processes projecting into the fenestrae (94-0). The palatine-pterygoid suture does not reach the posterior angle of suborbital fenestra (85-1). There are no swellings or palatinal bullae.

*Vomer*.—There is no trace of vomerine exposure on the palate (125-0; 126-0).

*Pterygoids*.—The pterygoids are badly crushed, particularly in the central area (close to the choanae) but, even if deformed, show well-developed, tall and prominent, posterior processes (98-0). There are no pterygoid bullae.

*Ectoperygoids*.—The ectopterygoids are separated from the toothrow by the maxilla (91-1) and their anterior process tapers to a point (109-0). Ectopterygoid-pterygoid suture without flexure (116-0). Ectopterygoids do not reach the posterior tip of lateral pterygoid flange (149-1).

## Lower jaw

*Preservation and general features*.—The lower jaw is not as deformed as the skull and it seems to be only minimally distorted, but it is less complete. It is represented by dentaries, splenials and an isolated fragment of a right angular. The lateral and ventral surface of the lower jaw is ornamented by evident furrows and pits.

*Dentaries*.—The left dentary lacks of the anterior lateral area, whereas both dentaries, as well the splenial, are posteriorly broken off (however, the right dentary is the most complete). Due to such incompleteness, the total number of dentary teeth could have been slightly higher than the number of preserved teeth positions, which is of 22 on the right dentary. The third alveolus is slightly smaller than the fourth and not confluent (52-1). The dentary is linear between teeth positions four and ten (68-2).

The symphysis extends posteriorly to the sixteenth dentary alveolus. The posterior region of both dentaries diverges gradually as in extant *Tomistoma* and not as widely as in *Gavialis* (moreover, there is no trace of an anterior extension of the surangular up to the level of the symphysis).

*Splenials*.—The splenials extend anteriorly to the level of at least the eleventh tooth position and are therefore involved in the symphysis for a little more than the length of five alveoli (as in *Tomistoma*); the posterior symphyseal area of left splenial does not show the presence of *foramen intermandibularis oralis* but a tiny foramen occurs in the same area of the right splenial probably because of the incompleteness of the medial bony surface. The presence of an anterior perforation for mandibular ramus of the fifth cranial nerve is therefore unknown and character 41 has been coded as "?"). The anteroposteriorly deep splenial symphysis is relatively wide and lacks an anterior constriction, showing a condition more similar to the one shown by extant *Gavialis* than to that of *Tomistoma* (43-3). The symphysis extends posteriorly to the middle of the sixteenth alveolus. Since the splenials are posteriorly broken it is not possible to assess with confidence the presence/absence of posterior foramina (42-?).

*Angular*.—An isolated fragment corresponds to a small ventral portion of right angular.

## Dentition

*Teeth*.—Tooth crowns are slender and acute but their morphology is peculiar due to the fact that there are no principal mesio-distal keels. Instead, there are several (up to 25) ridges, of similar development, on the entire surface (from the lower margin of the crown to its apex). The mesio-distal ridges are less pronounced in the posteriormost maxillary and dentary teeth (that are slightly less compressed than the previous ones). However, it is not possible to identify any labio-lingual compression. Tooth morphology is uniform in every tooth bearing bone. The crown length reaches 22 mm.

*Dentition pattern*.—The dentition can be considered pseudo-homodont since teeth are rather similar in shape and differ only slightly in size (89-4).

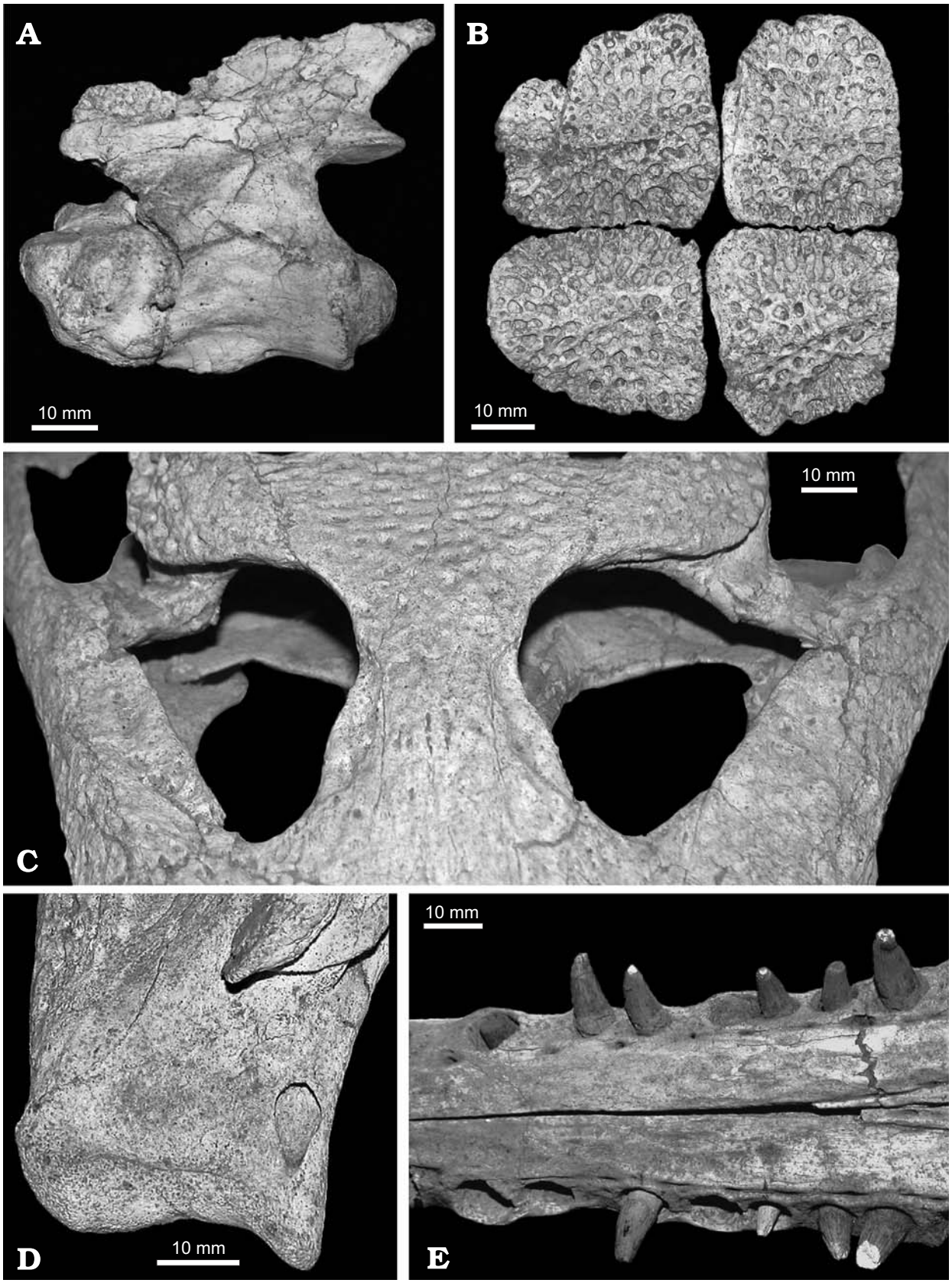


Fig. 6. Holotype of *Eosuchus lerichei* Dollo, 1907. IRSNB R 48, Jeumont, France, late Paleocene. **A**. Axis in left lateral view. **B**. Nuchal osteoderms in dorsal view. **C**. Detail of the orbital region of the skull showing the L-shaped deflected postorbital bars and the "step-like" structures characteriszing the antero-medial margin of the orbits. **D**. Detail of right quadrate showing the extremely enlarged foramen aereum. **E**. Detail of lower jaw showing the couplets of teeth and the asymmetrical alveolar arrangement.

The upper toothrow consists of 21/22 teeth (5 premaxillary teeth plus16 right and 17 left maxillary teeth), the lower one consists minimally of 22 teeth.

The arrangement of the dentary teeth and alveoli is unusual: if we compare the two dentaries, the arrangement (tooth positions and therefore interalveolar spaces) is asymmetrical and in some cases, on both dentaries, two teeth occluded in one single interdentary space of maxilla (at present it is not possible to occlude the jaws due to the deformation of the maxillae), and the alveoli are sometimes arranged in pairs (Fig. 6E). The pattern on the premaxillae and maxillae is more regular and symmetrical. Although size differences are minimal, the biggest tooth is the fourth on the premaxillae. Occlusal pits are not present either between teeth or lingually to them (absent for Dollo 1907 and Swinton 1937, but surprisingly present for Vasse 1993 that explicitly quotes Dollo).

The fourth dentary tooth occludes in a notch between premaxilla and maxilla (77-0) and the occlusion pattern can be coded as in-line (78-2).

### Forelimb

The distal epiphysis of the ulna and radius are missing, while the proximal ends are partly eroded. The length of the ulna fragment is 96 mm; that of the radius is 61 mm. The proximal surface of ulna shows a wide and rounded olecranon process (27-1). A carpal element, the ulnare, is 16 mm tall.

### Vertebrae

The axis and 3 cervical vertebrae (plus a neural arch fragment) are moderately deformed (asymmetrical) but rather complete. They all preserve closed neurocentral sutures.

The axis (Fig. 6A) is sutured to the atlas pleurocentrum (total length: 55 mm). Since the neural spine dorsal edge is missing, it is not possible to assess if its anterior area is horizontal or sloping, but the neural spine is high (= crested; 12-0), and posteriorly narrow (3-1), extending well beyond the small postzygapophyses. The neural arch lacks lateral processes (4-0). Diapophysial and parapophyseal articular facets are well developed on the intercentrum ("centre de l'Atlas" for Dollo 1907: 84). The odontoid process is robust and prominent. The centrum shows a modest ventral keel, developed in the anterior region (6-1) and not forked (19-1), and a prominently convex posterior end.

The three other cervicals are procoelous. One with the serial number "3" has a centrum length of 40 mm. It does not perfectly articulate with the axis and could be the fourth cervical vertebra (characters 8 and 9 have not been scored). It is well preserved and shows a medium-sized neural spine, overhanging posteriorly and with dorsal tip less than half the length of the centrum (cotyle not considered), distinct diapophysial and parapophysial articular facets, and a prominent keel shaped hypapophysis located under the cotyle.

The vertebra bearing the serial number "4" is 39 mm long (centrum length). Its left parapophysis is not complete and the hypapophysis is craniocaudally short but very wide and prominent. The neural spine is slightly shorter than that of "3" but more robust. It does not articulate with "3". The cervical vertebra with serial number "6" is not as well preserved as the previous one. The centrum length is 35 mm. The neural spine and right prezygapophysis are broken off, while the left pre- and postzygapophysis and the diapophysial and parapophysial articular facets are damaged. Although not complete, the hypapophysis is long both cranio-caudally and dorso-ventrally.

### Ribs

The 3 ribs (2 right and 1 left), showing well-developed tuberculum and capitulum and a shaft extending anteriorly to the articular processes, belong to the cervical region.

### Osteoderms

Altogether, there are fourteen osteoderms or fragments of them. The best-preserved osteoderms are two adjacent pairs, probably coming from the nuchal shield of the neck (Fig. 6B). They are nearly complete, square in shape (sides of about 45 mm) and markedly convex (folded along a sagittal line). The median side of each osteoderm is relatively thick and interlocks with that of the other member of the pair; the other sides do not show any interlocking structure and are rather thin. The sagittal thickening can be interpreted as a midline keel, and is better developed at the centre of the osteoderm. The entire dorsal surface (keel area included) is ornamented by relatively large, deep and subcircular pits; only the anterior edge of the second pair (whose position was caudal to that of the first— anterior—one) shows a small smooth articulation surface.

All other osteoderms are incomplete but one. They show an anterodorsal smooth articulation surface, a dorsal convexity and a ventral concavity fairly less developed than in some nuchal osteoderms previously described (thought not all have a ventral concavity). The best-preserved osteoderm does not have any keel. All the osteoderms are devoid of anterior processes or pegs. It has been not possible to anatomically allocate these osteoderms with confidence, and therefore the several characters concerning the dermal armor have not been scored.

# Phylogenetic analysis

The phylogenetic analysis (Fig. 7) is based on data matrix published by Brochu (1999), implemented by the direct observation of the holotype of *Eosuchus lerichei* and other taxa. The analysis also includes *Eosuchus minor* (coding from Brochu in press), *Dollosuchus dixoni* (unpublished data based on personal observation of the holotype IRSNB R 48) and the new taxa *Paratomistoma courti* Brochu and Gingerich, 2000 (codings available in the description paper), unnamed "Las Hoyas form" (coding from Buscalioni et al. 2001), *Allodaposuchus precedens* Nopcsa, 1928 (coding

from Buscalioni et al. 2001), *Piscogavialis jugaliperforatus* Kraus, 1998 (coding based on personal observation—P.P.—of the holotype SMNK 1282 PAL; see Appendix 1), *Siquisiquesuchus venezuelensis* Brochu and Rincón, 2004, and *Eothoracosaurus mississippiensis* Brochu, 2004 (codings available in the description papers); for character 140 we updated the coding for *Ikanogavialis*, *Gryposuchus*, and *Piscogavialis* according to the new state introduced by Brochu and Rincón (2004). Following Buscalioni et al. (2001) and Brochu (in press), three new characters have been added to the data matrix (see Appendix 1): characters 165 and 166 have been defined (with the same sequential number) by Buscalioni et al. 2001; character 167 follows character 165 by Brochu (in press).

The character codings of *Eosuchus lerichei*, *Dollosuchus dixoni*, and *Piscogavialis jugaliperforatus* are presented in Appendix 1.

Coding of *Allodaposuchus precedens* has been revised for characters 99 and 106 and therefore scored as "0" and "?" respectively (characters that in Buscalioni et al. 2001, were based on an earlier matrix version—Brochu 1997 and not 1999).

Codings of both *Bernissartia fagesii* and *Hylaeochampsa vectiana* have been taken from original Brochu's 1999 matrix. The status of characters 165 and 166 of *P. courti* has been evaluated on Brochu and Gingerich (2000) paper and scored as "1" and "?" respectively.

The coding for "Dormaal crocodyloid" follows Brochu (1999) and retains its original name even if is likely that such coding has been based on fossil material coming from the locality Orp-le-Grand in Belgium (the "Dormaal crocodyloid" is highly fragmentary).

The matrix, comprehensive of 73 taxa and 167 characters, was processed with PAUP 4.0b10* (Swofford 1999). The outgroup is represented by *Bernissartia fagesii* and *Hylaeochampsa vectiana*. Both ACCTRAN and DELTRAN optimization was performed with TBR in effect and 100 replicates of random addition sequence. Characters where treated as unordered.

# Results

The cladistic analysis recovered 8095 equally most parsimonious trees of 521 steps (Fig. 7). The strict consensus tree is 526 steps long with a CI = 0.401; RCI = 0.330; RI = 0.822; HI = 0.599. As with previous morphological/paleontological analyses, our study supports a placement of the living Indonesian false gharial *Tomistoma* within Crocodylidae and not within Gavialidae, as suggested by molecular evidences (Gatesy et al. 2003 and references therein). The general topology is basically congruent with those previously published by other authors (Brochu 1999, 2000, 2004; Brochu and Rincón 2004; Buscalioni et al. 2001; Hua and Jouve 2004) albeit some differences are discussed below.

# Discussion

The coding of *E. lerichei* here presented differs for few characters (reflecting different opinion on its morphology) from that published by Brochu (in press). The most important divergences concern the robustness of postorbital bar (70), the relationships between ectopterygoid and tooth row (91) and the shape of the palatine processes (118).

The robustness of postorbital bars in *E. lerichei* is partly hidden by their strong deformation, and although not as slender as, for example, modern *Alligator*, it seems that they are not as massive as in similarly sized *Gavialis gangeticus* (the only modern species with massive postorbital bars) or other fossil gavialoids.

*Eosuchus lerichei* shows ectopterygoids well separated from the toothrow by maxilla (91-1): the ectopterygoids extend anteriorly for less than two maxillary teeth (they are therefore short) and do not closely border the toothrow. This character, scored by Brochu (in press) as "0" for *E. lerichei* and *E. minor*, could be homoplasic within Gavialoidea. However, it should be probably better defined, since, among others, Recent *Gavialis gangeticus* and *Crocodylus niloticus* are quite different from each other and their condition should be not scored as "0" in both cases. Moreover, the status of character "91" as shown by "*Crocodilus clavirostris*" Morton, 1845 (Brochu in press: fig. 14: 2), a longirostrine crocodilian possibly referable to *E. minor* according to Brochu (in press), is clearly different from that of *E. lerichei*.

Although relatively narrow, palatine processes are slightly constricted medially and they are actually closer to the condition show by *C. rhombifer* (processes anteriorly broad) than to that of *Gavialis gangeticus* (anterior tip form a thin wedge); the condition of *Eosuchus lerichei* can be therefore considered as a particularly narrowed U-shaped condition (118-0). Brochu (in press) scored this character as having state "1" in *E. lerichei* and *E. minor*. Actually, *E. minor* USNM299730 (Brochu in press: fig. 9: 2) seems to have a condition similar to the one here described (although palatine process is split along the midline) while "*Crocodilus clavirostris*" ANSP 10079 (Brochu in press: fig. 14) shows "much more acute" wedged palatine process.

Despite these differences in the evaluation of some character states, the general topological results of our analysis do not differ from that of Brochu (in press) for the taxa here considered. *E. lerichei* and *E. minor* have a basal position among gavialoids and are sister taxa; the strong similarities between these two taxa justify their inclusion in the same genus. This analysis does not allow resolution of the polytomy including the South American gharials (*Gryphosuchus*, *Ikanogavialis*, *Piscogavialis*, and *Siquisiquesuchus*). Moreover, in the phylogenetic framework here proposed, *Eogavialis africanum* (Andrews, 1901) from the Eocene–Oligocene of the Fayum depression (Egypt) is more basal than *Argokampsa krebsi* Hua and Jouve, 2004 from Paleocene sediments of Morocco. Such apparent stratigraphic incongruence would not be signifi-

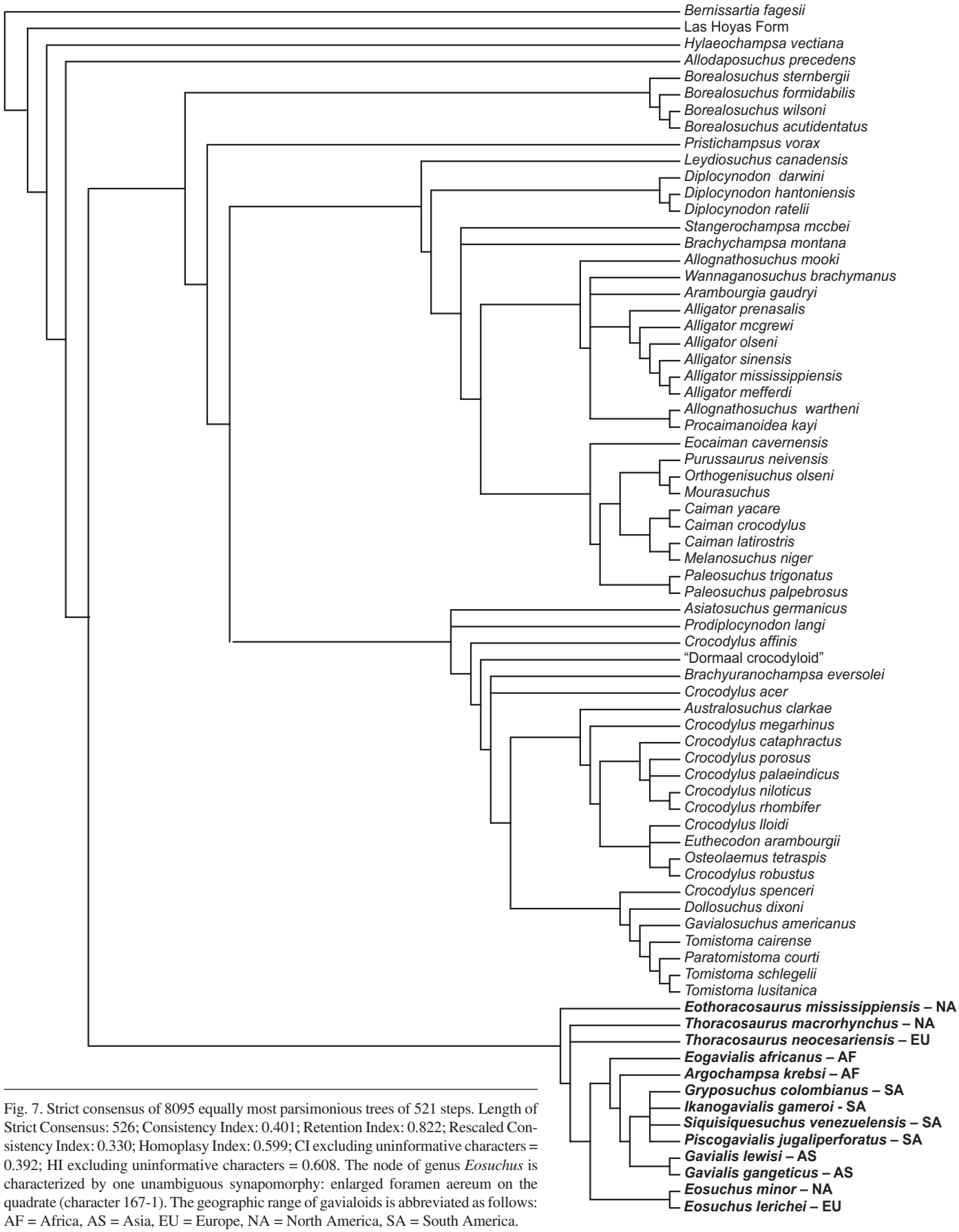


Fig. 7. Strict consensus of 8095 equally most parsimonious trees of 521 steps. Length of Strict Consensus: 526; Consistency Index: 0.401; Retention Index: 0.822; Rescaled Consistency Index: 0.330; Homoplasy Index: 0.599; CI excluding uninformative characters = 0.392; HI excluding uninformative characters = 0.608. The node of genus *Eosuchus* is characterized by one unambiguous synapomorphy: enlarged foramen aereum on the quadrate (character 167-1). The geographic range of gavialoids is abbreviated as follows: AF = Africa, AS = Asia, EU = Europe, NA = North America, SA = South America.

cantly affected by a reassessment of the age of *Argochampsa*: following Noubhani and Cappetta (1997), Hua and Jouve (2004) refer the horizon of the holotype bearing strata to the "Dano-Thanetian boundary", but a more precise chronological allocations might be possible since the International Stratigraphic Commission (2004) subdivides the Paleocene into three stages: Danian, Selandian, and Thanetian (Gradstein et al. 2005).

The apparent incongruence is probably due to a fossil gap that affects the Paleogene (between the "extinction" of thoracosaurs and the appearance of *Eogavialis*; Brochu 2004). *Argochampsa* and *Eosuchus* spp. partially fill this gap but more Paleocene material from Africa or elsewhere would better clarify their actual phylogenetic relationships.

The relationships and monophyly of *Eosuchus* have been thoroughly discussed by Brochu (in press) and will briefly examined here.

*Eosuchus* is closely related to *Gavialis* than are *Eothoracosaurus* and *Thoracosaurus,* but it is basal relative to *Eogavialis*, and the South American clade.

*E. lerichei* and *E. minor* share only one unambiguous synapomorphy in the adopted matrix: an extremely developed foramen aereum on the quadrate, a character already noticed by Dollo (1907: 84; "Canal de Stannius […] énorme") and later by Swinton (1937: 10). The holotype of *E. minor*, YPM 282, shows an extremely wide foramen aereum (Norell and Storrs 1986) but the foramen aereum is visibly more anteroposteriorly elongated than *E. lerichei*. Moreover, the dentary alveoli of both taxa, although showing some degree of irregularity, are arranged in couplet, a condition not known in any other crocodylian. Further characters are listed in the diagnosis section.

Differences between *E. lerichei* and *E. minor* seem to be related to the derived state of some characters in the European form: the postorbital bar is not as massive as in other gavialoids (70-1), frontoparietal suture is entirely on skull table (81-2), ectopterygoid are separated from maxillary toothrow (91-1). At the same time, the state of characters 4 (lack of diapophysis on axis neural spine) and 118 (palatine processes not thin wedged) are here interpreted as possible reversals. *E. lerichei* seems to be slightly more derived than *E. minor*.

In addition, *E. lerichei* shows a peculiar "step" like structure on the orbital margin of prefrontals: such a "step" has not been explicitly described for *E. minor*; from the available pictures it seems to be present but possibly less developed; such a character could represent a further diagnostic character of the genus.

Complete closure of the cervical neurocentral sutures (Brochu 1996) indicates that the holotype of *Eosuchus lerichei* was morphologically mature at death; therefore this species was a relatively small-sized crocodylian probably reaching a total length of about 350 cm. If *E. minor* was a species of similar size, it is rather likely that "*Crocodilus clavirostris*" does not belong to the same species (see Brochu in press for a discussion of *C. clavirostris* taxonomy).

That both *E. lerichei* and *E. minor* come from marine settings represents further evidence for the salt-water tolerance that characterized the earliest stages of gavialoid evolutionary history. Such physiological characteristics can be indirectly deduced by fossils, since all known Cretaceous and Paleocene gavialoids have been retrieved from coastal-marine deposits. Thoracosaurs are among of the few Late Cretaceous crocodylians not restricted to a single continent (Buscalioni et al. 2003), having inhabited both North America and Europe. *Eosuchus* shows a similar pattern in the Paleocene. That *E. lerichei* shows few character states derived compared to those of *E. minor*, could suggest an eastward dispersal from North America to Northern Europe before the Paleocene–Eocene boundary, but the distribution and chronological allocation of the fossil remains so far discovered can not rule out an alternative scenario in which *E. minor* (or a form close to) might have inhabited both the continents and evolved into or was replaced by *E. lerichei* in Europe at least.

Moreover, the historical biogeography of Gavialoidaea seems to suggest that salt-water intolerance could be a relatively recent acquisition of Gavialoidea.

The only living gavialoid, *Gavialis gangeticus* from the Indian region occurs in fluvio-lacustrine environments and shows a reduced number of lingual glands of very low secretory capacity (see Leslie and Taplin 2001 and references therein). On the other hand, the distribution of fossil gavialoids is best explained assuming multiple transoceanic dispersals. If we assume that gavialoids originated along the North Atlantic margin during the Late Cretaceous, then we have to assume multiple dispersals to Europe and to Africa; South America has been inhabited at least since the beginning of the Miocene and it was probably colonized from an African stock (not necessarily only once), while it is not clear if Asia was reached from the Old or the New World, although an Old World origin seems to be more likely (among others, Buffetaut 1982; Langston and Gasparini, 1997; Brochu 2001 b, 2004; Brochu and Rincón 2004; Jouve 2004). The earliest Asian gavialids are early Miocene in age (Piras and Kotsakis in press) and all Indo-Pakistani remains come from fluvio-lacustrine or fluvio-deltaic environments. It is striking that no clear transoceanic dispersals from the Indo-Pakistani region (that can testify for the crossing of a significant marine barrier) has been recorded. Even if we cannot exclude that salt intolerance arose independently in South American and African gavialoids (since many of the post-Paleocene remains come from continental settings), the fossil record suggests that the adaptation to fresh-water is a comparatively recent acquisition among Gavialoidaea and that it strongly influenced the history of the lineage that lead to the living *Gavialis gangeticus.*

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# Appendix 1

Full character codings for *E. lerichei*, *D. dixoni*, and *P. jugaliperforatus* (see section "Phylogenetic analysis" for details) followed by codings of characters 165, 166, and 167 for all the taxa included in this analysis; definition for characters 165 and 166 available in Buscalioni et al. (2001); definition for character 167 follows character 165 by Brochu (in press): quadrate foramen aereum small or absent (0), or comparatively large (1).

*Eosuchus lerichei*
??10? 1???? ?0??? ??11? ????? ?1??? ????0 ????? ??3?? ????? ?11?? ????? ????? ??201100?0 (12)021? 20011 00040 11002 ?00?0 0?100 ?0000 00?0? 000?0 0?000 0???? ?00?0 ?0?01 10001 00?10 1?0?? ????? 0?0?? ?1

*Dollosuchus dixoni*
?010? 1(02)??0 ?0??? ?110? ???01 11?1? ?000? ????? ?00?? (12)0001 111?? ???00 11010 0?2?1 100?0 ?021? 20?01 00010 01102 ?01?0 0?1?0 000?0 030?? 0011? 0?100 0???? ???10 ???01 10001 1??10 001?? ????? 010?? ?0

*Piscogavialis jugaliperforatus*
????? ????? ????? ????? ????? ????? ???1? ????? ??3?? ?00?1 011?? ????? 01??? ??210 100?0 00211 20011 00040 01?02 ?12?0 00100 ?0000 00??? 001?0 00000 00??0 00000 ???12 10001 0??00 100?? ????? 0?0?? 10

| | | | |
|---|---|---|---|
| *Bernissartia fagesii* | 000 | *Caiman crocodylus* | 110 |
| *Hylaeochampsa vectiana* | 000 | *Caiman latirostris* | 110 |
| *Allodaposuchus precedens* | 000 | *Melanosuchus niger* | 110 |
| *Borealosuchus formidabilis* | 110 | *Paleosuchus trigonatus* | 110 |
| *Borealosuchus wilsoni* | ??0 | *Paleosuchus palpebrosus* | 110 |
| *Borealosuchus acutidentatus* | ??0 | *Crocodylus cataphractus* | 110 |
| *Borealosuchus sternbergii* | ?10 | *Crocodylus niloticus* | 110 |
| *Leydiosuchus canadensis* | ??0 | *Crocodylus porosus* | 110 |
| *Thoracosaurus macrorhynchus* | ??0 | *Crocodylus rhombifer* | 110 |
| *Eogavialis africanus* | ?10 | *Crocodylus palaeindicus* | ??0 |
| *Gryposuchus colombianus* | ??0 | *Osteolaemus tetraspis* | 110 |
| *Gavialis lewisi* | ?10 | *Crocodylus robustus* | 110 |
| *Gavialis gangeticus* | 110 | *Crocodylus lloidi* | ?10 |
| *Pristichampsus vorax* | ?10 | *Crocodylus megarhinus* | ??0 |
| *Diplocynodon hantoniensis* | 110 | *Euthecodon arambourgii* | ??0 |
| *Diplocynodon ratelii* | 110 | *Tomistoma schlegelii* | 110 |
| *Diplocynodon darwini* | 110 | *Tomistoma lusitanica* | ?10 |
| *Stangerochampsa mccbei* | ?10 | *Gavialosuchus americanus* | 110 |
| *Brachychampsa montana* | ?10 | *Tomistoma cairense* | ??0 |
| *Alligator sinensis* | 110 | *Crocodylus spenceri* | ??0 |
| *Alligator mississippiensis* | 110 | *Brachyuranochampsa eversolei* | ?10 |
| *Alligator mefferdi* | 110 | "Dormaal crocodyloid" | ??0 |
| *Alligator olseni* | ??0 | *Crocodylus acer* | ?10 |
| *Alligator mcgrewi* | ?10 | *Crocodylus affinis* | ?10 |
| *Alligator prenasalis* | 110 | *Asiatosuchus germanicus* | 110 |
| *Allognathosuchus wartheni* | ?10 | *Prodiplocynodon langi* | 110 |
| *Allognathosuchus mooki* | ?10 | *Australosuchus clarkae* | ??0 |
| *Wannaganosuchus brachymanus* | ?10 | Las Hoyas Form | ?00 |
| *Procaimanoidea kayi* | ??0 | *Paratomistoma courti* | 1?0 |
| *Arambourgia gaudryi* | ?10 | *Argochampsa krebsi* | ?00 |
| *Eocaiman cavernensis* | ??0 | *Eosuchus minor* | ??1 |
| *Purussaurus neivensis* | ??0 | *Eothoracosaurus mississippiensis* | ?10 |
| *Orthogenisuchus olseni* | ??0 | *Thoracosaurus neocesariensis* | ??0 |
| *Mourasuchus* | ??0 | *Ikanogavialis gameroi* | ??0 |
| *Caiman yacare* | 110 | *Siquesiquesuchus venezuelensis* | ??? |